EFFECT OF DAY LENGTH AND TEMPERATURE ON THE FLOWERING AND GROWTH OF FOUR SPECIES OF GRASSES[1]

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INTRODUCTION

In attempts to carry on physiological investigations with native grasses in the greenhouse during the winter months, the writer has often encountered difficulty in obtaining flower production and good vegetative growth. Some of the grasses when grown under winter greenhouse conditions produce a low tufted top growth and never send up flower stalks. Other species produce only a few leaves and then seem to stop growing until late in the winter or early spring. As a result of the work of Garner and Allard (*4*, *5*, *6*),[2] Tincker (*9*, *10*), Adams (*1*, *2*, *3*), Gilbert (*7*), Thompson (*8*), and others, it was thought that lengthening the day or varying the temperature might bring about increased growth and production of flower stalks in those species that usually do not grow well in the greenhouse during the winter.

In this paper are presented the results of experiments on the effects of different day lengths and temperatures on bluestem (*Agropyron smithii* Rydb.), locally known as western wheatgrass, blue grama (*Bouteloua gracilis* (H. B. K.) Lag.), bluejoint turkeyfoot (*Andropogon furcatus* Muhl.), locally known as big bluestem, and switchgrass (*Panicum virgatum* L.). The first two species are the most common grasses in the short-grass plains and make fairly good growth but rarely flower in the greenhouse during the winter season. The last two species are common in the tall-grass prairies and, at least at Cheyenne, Wyo., make very little growth under winter greenhouse conditions.

METHODS

Three series of experiments were carried out, the first and third during the winter when the days are naturally short and greenhouse temperatures can be kept low, and the second in the summer when the days are naturally long and greenhouse temperatures become high during the day. In the first series plants of *Agropyron smithii* and *Bouteloua gracilis* were grown in seed flats 16 by 24 by 4 inches, 100 plants to a flat, from October 21, 1934, to March 21, 1935. The plants in this series (series 1) were grown in 8-hour, 20-hour, and natural day lengths at a temperature of 60° F. and in a natural day length at a temperature of 75°. In the second series, plants of the same two species

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[2] Italic numbers in parentheses refer to Literature Cited, p. 670.

were grown in seed flats, 77 plants to a flat, in an 8-hour and a 20-hour day, from June 11, 1935, until October 4, 1935. During this period the temperature was maintained as close to 80° as possible, although during the middle of the day it was often several degrees higher. The third series contained plants of *Agropyron smithii*, *Andropogon furcatus*, *Bouteloua gracilis*, and *Panicum virgatum*. These plants were grown in seed flats from November 20, 1936, to March 24, 1937. The plants were all thinned to 50 per flat and grown under the following six conditions, with duplicate flats of each species placed in each treatment.

(1) In a natural, or short, day length at a day and night temperature of 75° F.
(2) In a natural day length at a day temperature of 75° F. and a night temperature of 60°.
(3) In an 18-hour, or long, day length at a day and night temperature of 75° F.
(4) In an 18-hour day at a temperature of 75° F. during the day and a night temperature of 60°.
(5) In a natural day length until January 20 and then in an 18-hour day length until March 24, at a day and night temperature of 75° F.
(6) In an 18-hour day length until January 20 and then in a natural day length until March 24 at a day and night temperature of 75° F.

The desired temperatures in the three series of experiments were maintained by hand operation of the greenhouse ventilators. This method admittedly allows for some variation, but except for the summer series this was never more than 5° F., according to the thermograph records that were kept. The night temperature of 60° used in series 3 was obtained by removing the plants from the greenhouse to a propagating house for the required length of time.

The 18- and 20-hour day lengths were obtained by burning incandescent lamps from shortly before sundown for as many hours as were necessary to give the required day length. The intensity of the radiation of the incandescent lamps at the surface of the soil was 35 foot-candles. The areas lighted by the lamps were screened so as to prevent any stray radiations from reaching areas that were to be kept dark. The 8-hour day length was maintained by covering the plants with a lightproof canvas from 4 p. m. until 8 a. m. daily. This canvas was suspended on a frame 54 inches high, closed at either end by wallboarding that could be removed during the day. It was not possible to observe any light in the compartment thus formed. The temperature inside never exceeded that of the rest of the greenhouse by more than 2° F.

By thoroughly mixing the soil before placing it in the flats in all three experiments, care was taken to insure that no differences in the soil existed between treatments.

According to information supplied by the United States Weather Bureau, the average length of daily sunlight during the time the plants were being grown in the winter was about 10¼ hours. Thus the natural day length in the winter will be considered a short day.

The dry weight per plant was used as the criterion of growth of the plants subjected to the various treatments. The dry weights were determined by carefully washing the soil from the plants, separating the roots from the tops, placing both in an oven at 100° C. for an hour, and then drying them to constant weight at 80°.

EXPERIMENTAL RESULTS AND DISCUSSION

EFFECT OF DAY LENGTH AND TEMPERATURE ON FLOWERING

The number of days elapsing between the date of planting and the date on which at least three plants in a given treatment showed flower stalks are given in table 1. The results presented here indicate that *Agropyron smithii* is a long-day plant and that the proper temperature alone will not bring about flowering. This is brought out by the fact that under the conditions of these experiments plants of this species flowered in an 18- or 20-hour day when the temperatures in which they were growing ranged from 60° to 80° F. but failed to bloom when growing at these temperatures in an 8- or 10-hour day. It will be noted that plants of this species in series 3 failed to bloom in an 18-hour day when the night temperature was lowered from 75° to 60°. This failure to flower may have been due entirely to the low temperature, but since the plants of this series that did flower did so on the last day of the experiment it seems possible that the plants were not grown long enough to reach the flowering stage.

TABLE 1.—*Number of days between the date of planting and the appearance of first bloom of different grasses grown in different day lengths and temperatures*

Treatment		Time from planting to blooming in indicated species			
Day length	Temperature conditions	*Agropyron smithii*	*Andropogon furcatus*	*Bouteloua gracilis*	*Panicum virgatum*
	°F.	Days	Days	Days	Days
Series 1 (winter):					
8-hour day	60	(1)		(1)	
Natural, or 10-hour, day	60	(1)		(1)	
20-hour day	60	149		(1)	
Natural, or 10-hour, day	75	(1)		93	
Series 2 (summer):					
8-hour day	80	(1)		72	
20-hour day	80	98		100	
Series 3 (winter):					
Natural, or 10-hour, day	75 throughout	(1)	(1)	70	72
Natural, or 10-hour, day	75 day; 60 night	(1)	101	(1)	93
18-hour day	75 throughout	120	(1)	113	(1)
18-hour day	75 day; 60 night	(1)	(1)	(1)	(1)
10-hour, 2 months; 18-hour, 2 months.	75 throughout	(1)	(1)	70	(1)
18-hour, 2 months; 10-hour, 2 months.	75 throughout	(1)	(1)	87	(1)

[1] Failed to bloom.

As shown in table 1, plants of *Bouteloua gracilis* flowered in an 18- and 20-hour day as well as in an 8- or 10-hour day when the temperature remained at 75° F. or above, but failed to flower in any day length when the temperature dropped to 60° for even a few hours daily. The plants grown in the shorter day lengths flowered earlier than those grown in the longer day lengths. These results indicate that *B. gracilis* is an indeterminate type of plant as far as its blooming response to day length is concerned and that a fairly high temperature is necessary to produce flowering.

Plants of *Andropogon furcatus* bloomed in the 10-hour day at a temperature of 75° F. during the day and 60° during the night, but

did not bloom in this short day when the temperature was kept at 75° throughout, nor did the plants of this species bloom in the 18-hour, or long, day. These results seem to indicate that *A. furcatus* is a short-day plant and that temperature alone does not determine whether it will flower. The plants of this species grown at a temperature of 75° in the short day may not have flowered because of the extremely small growth they made, having a total dry weight of only 23 mg.

Plants of *Panicum virgatum* bloomed when grown in a short day, regardless of the temperature, although lowering the temperature at night retarded the blooming date somewhat. This would indicate that *P. virgatum* is a short-day plant and that the temperatures used in this experiment have little influence in determining whether or not these plants will flower.

In setting up the treatments in which the plants were grown, first in a short day and then in a long day or first in a long day and then in a short day, it was thought that the day length unfavorable to flowering when applied first would cause the plants to vegetate and that then changing to the day length favorable for flowering would result in these plants coming into flower very rapidly. However, it will be noted from table 1 that only the plants of *Bouteloua gracilis* flowered in these treatments and that the plants of this species were able to flower in either a continuous long or a continuous short day. These results seem to show for the other three grasses under the conditions of these experiments that the effect of growing them for 2 months in a day length unfavorable for blooming was not overcome by growing them afterward for 2 months in a day length favorable for blooming. They also show that a day length unfavorable for blooming was able quickly to overcome the effects of growing the plants for 2 months in a day length favorable for blooming. For example, plants of *Panicum virgatum* growing in a long day did not flower while those growing in a short day flowered in 72 days. Yet when plants growing in the short day for 61 days were placed in a long day they did not flower, nor did the plants of this species flower when transferred to a short day after being in a long day for 2 months.

The classification of *Agropyron smithii* as a long-day plant, *Andropogon furcatus* and *Panicum virgatum* as short-day plants, and *Bouteloua gracilis* as a plant of indeterminate day length is borne out by the time of the year in which these plants come into flower when growing under natural conditions. Plants of *A. smithii* bloom in the latter part of June when the days are longest. Plants of *B. gracilis* will send up flower stalks throughout the summer. Plants of *A. furcatus* and *P. virgatum* come into flower around the middle of August, when the days are becoming shorter.

EFFECT OF DAY LENGTH AND TEMPERATURE ON GROWTH

The dry-weight determinations on the plants of the first series were ruined by an overheated oven and so cannot be presented. The dry weights per plant of the roots, tops, and total plant of the species grown in series 2 and 3 are shown in tables 2 and 3, respectively. The values presented in table 3 are the means of the two replications of each species in each treatment. In both series, with one exception, the weights of the individual parts of a plant of one species always

varied in the same direction with change in treatment. Thus, if the roots of the plants of one species increased when the day length was increased, the tops also increased in dry weight and naturally the entire plant showed the same trend. This makes it possible to discuss together instead of separately the results of the treatments of the plants of the different species.

TABLE 2.—*Dry weight per plant of Agropyron smithii and Bouteloua gracilis (series 2) grown in the summer of 1935 under different day lengths at 80° F.*

Species and treatment	Dry weight per plant		
	Root	Top	Total
Agropyron smithii:	*Gram*	*Gram*	*Gram*
8-hour day	0.056	0.131	0.187
20-hour day	.053	.124	.177
Bouteloua gracilis:			
8-hour day	.255	.436	.691
20-hour day	.289	.620	.909

TABLE 3.—*Dry weight per plant of grasses of series 3 when grown in different day lengths and temperatures*

Species and plant part	Dry weight per plant under indicated conditions					
	Normal or 10-hour day		18-hour day		10-hour day, 2 months; 18-hour day, 2 months; 75° F. throughout	18-hour day, 2 months; 10-hour day, 2 months; 75° F. throughout
	75° F. throughout	75° F. day, 60° F. night	75° F. throughout	75° F. day, 60°F. night		
Agropyron smithii:	*Gram*	*Gram*	*Grams*	*Gram*	*Gram*	*Gram*
Roots	0.176	0.235	0.194	0.228	0.236	0.243
Tops	.312	.420	.346	.372	.408	.375
Total	.488	.655	.540	.600	.644	.618
Andropogon furcatus:						
Roots	.009	.023	.311	.324	.030	.113
Tops	.014	.033	.545	.587	.098	.155
Total	.023	.056	.856	.911	.128	.268
Bouteloua gracilis:						
Roots	.184	.091	.315	.206	.235	.323
Tops	.560	.218	.825	.571	.731	.652
Total	.744	.309	1.140	.777	.966	.975
Panicum virgatum:						
Roots	.010	.074	.299	.223	.024	.101
Tops	.006	.053	.721	.504	.052	.063
Total	.016	.127	1.020	.727	.076	.164

The results of the dry-weight determinations (table 2) indicate that day length has little effect on the growth of plants of *Agropyron smithii*, provided the temperature is kept constant. This is brought out by the fact that in series 2 the plants of this species had about the same dry weight when grown in either the long or the short day and that in series 3, when grown at a temperature of 75° F. throughout, the plants in the long day had a slightly greater dry weight than those

in the short day but, when grown at a night temperature of 60°, the plants in the short day had a greater dry weight. The variations obtained between replications in series 3 indicate that not much importance can be attached to the differences noted between the dry weights of the plants growing in the different day lengths at the same temperature.

The results presented in table 3 also indicate that reducing the temperature at night causes an increase in the growth of plants of *Agropyron smithii*, since the plants growing in the low night temperature had the greater dry weight in both day lengths. This increase may be due to the reduced respiration rate occurring at the lower temperature, which would mean that less of the material manufactured during the day would be respired away at night. It can be seen that the plants in the short day showed a greater increase in dry weight when subjected to the lower temperatures than did the plants in the long day. This may be due to the fact that the former were in the low temperature for about 14 hours daily and the latter for only 6 hours daily. No explanation can be offered as to why the plants of *A. smithii* that were grown in a short day and then in a long day or were grown in a long day and then in a short day had somewhat greater dry weights than the plants grown continuously in a long or a short day.

The results of the dry-weight determinations on plants of *Andropogon furcatus* (table 3) require little discussion. They show that increasing the length of day greatly increases the growth or dry weight of the plants of this species, regardless of the temperature used. They also indicate that lowering the night temperature increases the dry weight of the plants, although not to the extent that increasing the day length does. This increase in dry weight in the lower night temperature might possibly be explained on the basis of reduced respiration rate, as in the case of plants of *Agropyron smithii*.

The results of the dry-weight determinations on plants of *Bouteloua gracilis* (tables 2 and 3) show that plants of this species are capable of making fairly good growth in either a long or a short day, but that increasing the day length markedly increases the growth of the plants, provided the temperature remains constant. The fact that the dry weights of the plants grown first in a short day and then in a long day or first in a long day and then in a short day were about intermediate to the dry weights of the plants grown throughout in a long or a short day indicates that a short day length is not so detrimental to the growth of this species as it is to that of *Andropogon furcatus* and *Panicum virgatum*. In the case of these latter species the dry weights of the plants grown in a short day and then in a long day or in a long day and then in a short day were nearer to those of the plants grown entirely in the short day.

It is interesting to note that lowering the night temperature in which the plants of *Bouteloua gracilis* were growing caused a reduction in the dry weight of the plants in both day lengths. It can also be seen that reducing the night temperature reduced by more than half the dry weights of the plants growing in the short day, but reduced by only a third those of the plants growing in the long days. These results would seem to indicate that plants of this species require a higher temperature than those of the other species for their growth

and that lowering the night temperature to 60° F. interferes with their metabolic processes to such an extent that the ensuing reduction in food production cannot be balanced by any reduced respiration rate that may result from the lower temperature. This is further borne out by the fact that the plants growing in the short day, which were subjected to the low temperatures for 14 hours daily, suffered a greater reduction in their dry weight than the plants growing in a long day, which were subjected to the low temperatures for only 6 hours daily. It will be remembered that the plants growing in the low night temperatures were the only ones that did not flower. This would further emphasize the high-temperature requirement of plants of *B. gracilis*.

The results of the dry-weight determinations on the plants of *Panicum virgatum* (table 3) show that the growth of this species is much greater in a long day than in a short day, since the dry weights of the plants under both temperature conditions were much greater in the long day. The results also indicate that lowering the temperature from 75° to 60° F. during the night increases the growth of the plants in a short day but decreases their growth in a long day.

The ratios obtained by dividing the dry weights of the roots by the dry weights of the tops of the plants grown in series 2 and 3 are shown in table 4. These results indicate that day length affects the relative growth of the roots as compared to that of the tops of plants of *Andropogon furcatus* and *Panicum virgatum* but not of *Agropyron smithii* and *Bouteloua gracilis*. Thus the root-top ratios of the former two species were greater in the short days than in the long days under both temperature conditions, but the root-top ratios of the latter two species did not differ significantly in the two day lengths. There is some evidence that changing the plants from a long day to a short day tended to increase the proportion of roots produced more than did changing the plants from a short day to a long day. This is brought out by the fact that the root-top ratios of the plants of all the species worked with were greater when the plants were grown in a long day for 2 months and then in a short day for 2 months than when they were grown in a short day for 2 months and then in a long day for 2 months. However, plants of *A. furcatus* and *P. virgatum* showed much greater differences in root-top ratios between these two treatments than did the plants of *A. smithii* and *B. gracilis*.

TABLE 4.—*Root-top ratio of plants of grasses of series 2 and 3 when grown in different day lengths and temperatures*

Treatment		Root-top ratio of indicated species			
Day length	Temperature conditions	*Agropyron smithii*	*Andropogon furcatus*	*Bouteloua gracilis*	*Panicum virgatum*
Series 2 (summer):	°F.				
8-hour day	80	0.43	----------	0.58	----------
20-hour day	80	.43	----------	.47	----------
Series 3 (winter):					
Natural, or 10-hour, day	75 throughout	.56	0.64	.33	1.67
Natural, or 10-hour, day	75 day, 60 night	.56	.70	.42	1.40
18-hour day	75 throughout	.56	.57	.38	.41
18-hour day	75 day, 60 night	.61	.55	.36	.44
10-hour, 2 months; 18-hour, 2 months.	75 throughout	.58	.31	.32	.46
18-hour, 2 months; 10-hour, 2 months.	75 throughout	.65	.73	.50	1.60

The results also indicate that a low night temperature has little or no effect on the relative amounts of roots and shoots produced by the plants, since the root-top ratios of the plants of the four species did not differ appreciably when grown in a high or a low night temperature in the same day length.

The plants of *Agropyron smithii*, *Andropogon furcatus*, *Bouteloua gracilis*, and *Panicum virgatum* after being grown for 11 weeks at

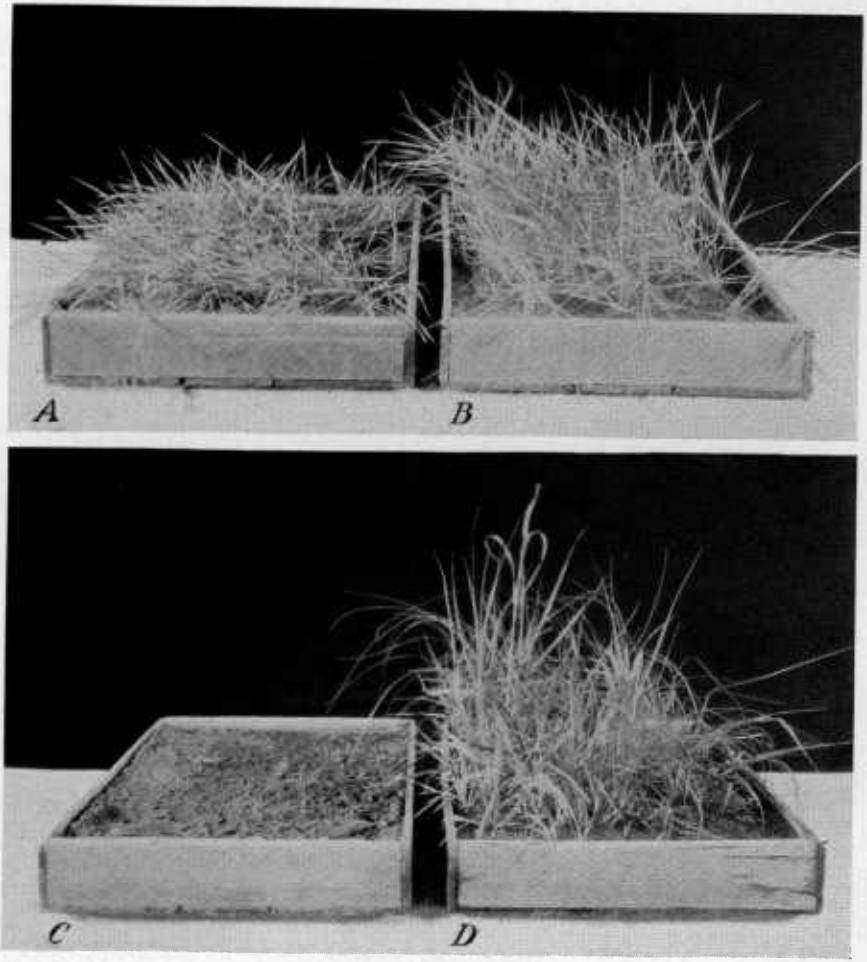

FIGURE 1.—Plants grown for 11 weeks at 75° F.: *Agropyron smithii* grown (*A*) in a 10-hour day and (*B*) in an 18-hour day; *Andropogon furcatus* grown (*C*) in a 10-hour day and (*D*) in an 18-hour day.

75° F. throughout, some in a 10-hour and some in an 18-hour day, are shown in figures 1 and 2. The exceedingly poor growth made by the plants *A. furcatus* and *P. virgatum* in the 10-hour day is brought out in figure 1, *C*, and figure 2, *C*. Figures 1 and 2 also show that a long day increased the height of the plants of all four species under investigation. However, there was no significant difference between the dry weights of the plants of *A. smithii* grown in the two treatments.

CONCLUSIONS

In general, the results presented in this paper indicate that the naturally short days are, at least in part, responsible for the failure of

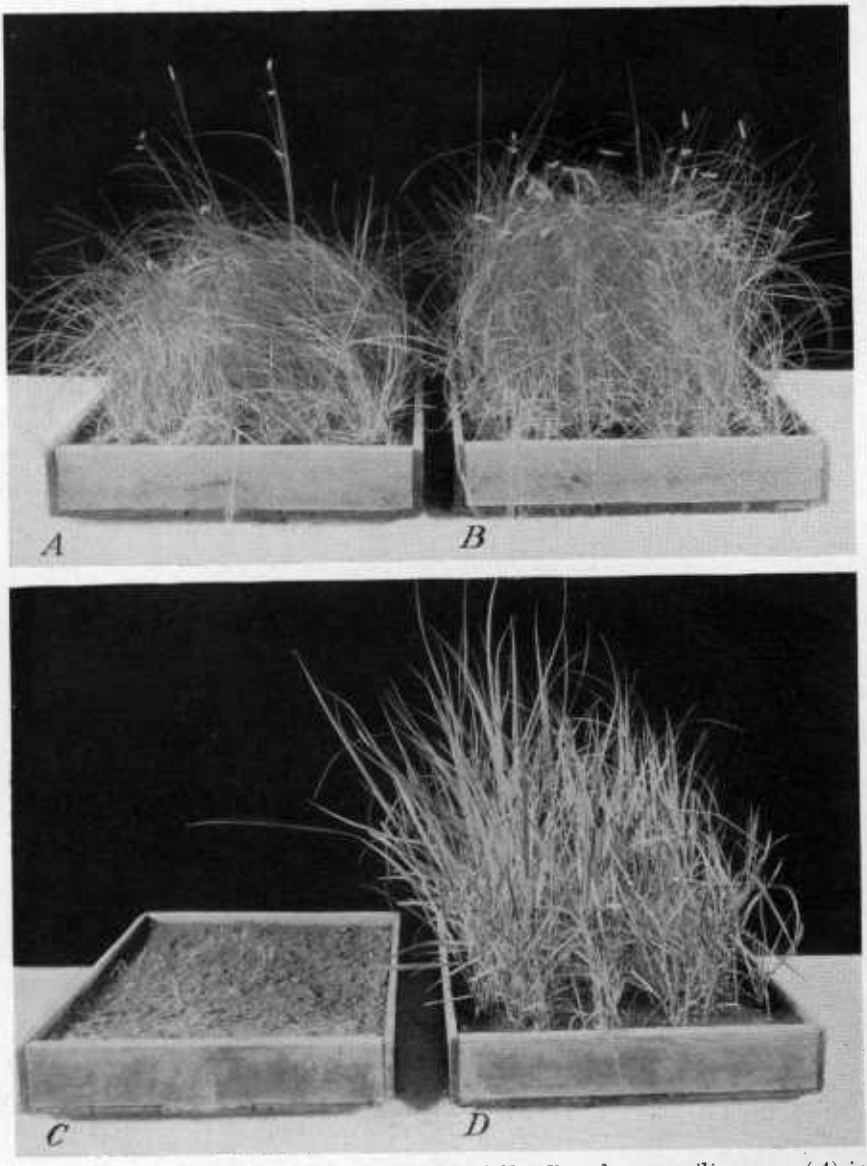

FIGURE 2.—Plants grown for 11 weeks at 75° F.: *Bouteloua gracilis* grown (*A*) in a 10-hour day and (*B*) in an 18-hour day; *Panicum virgatum* grown (*C*) in a 10-hour day and (*D*) in an 18-hour day.

plants of *Agropyron smithii* to bloom and of plants of *Andropogon furcatus* and *Panicum virgatum* to grow well in the greenhouse during the winter. This conclusion is based on the fact that plants of *A.*

smithii bloomed and the plants of *A. furcatus* and *P. virgatum* made good growth when the day length was increased by burning incandescent lamps for several hours each night. The results also tend to show that failure of plants of *Bouteloua gracilis* to flower may have been due to too low temperatures, since the plants of this species bloomed in both long and short days when the temperature was maintained at 75° F. but failed to bloom when the temperature was reduced to 60° for a few hours during the night.

SUMMARY

Plants of *Agropyron smithii* Rydb., *Andropogon furcatus* Muhl., *Bouteloua gracilis* (H. B. K.) Lag., and *Panicum virgatum* L. were grown in the greenhouse under different conditions of day length and temperature. Records were taken on the number of days between planting and the appearance of the first bloom, on the dry weights, and on the root-top ratios of the plants growing under the different conditions.

The results on the number of days required by the plants to flower indicate that *Agropyron smithii* is a long-day plant, *Bouteloua gracilis* is a plant of indeterminate day length, and *Andropogon furcatus* and *Panicum virgatum* are short-day plants.

The dry weights of the plants of *Agropyron smithii* were not affected by the day length, but in the other species the plants growing in the long days had the greater dry weight.

A low night temperature increased the dry weights of the plants of *Agropyron smithii* and *Andropogon furcatus* in both long and short days and also increased the dry weights of the plants of *Panicum virgatum* growing in a short day, but it decreased the dry weights of the plants of *Bouteloua gracilis* growing in both day lengths and also decreased that of plants of *P. virgatum* growing in a long day.

The root-top ratios of the plants of *Andropogon furcatus* and *Panicum virgatum* were greater in the short days than in the long days. No marked difference between the ratios of the plants of the other two species growing in the different day lengths was observed.

There was no significant difference between the root-top ratios of the plants of the four species when grown in a low night temperature and in a high night temperature in either day length.

The results, in general, indicate that day length and temperature markedly affect the growth and flower production of these four grasses and that good growth and blooming can be obtained in the greenhouse in the winter by properly controlling, among other things, these two factors.

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